

Species richness, hotspots, and the scale dependence of range maps in ecology and conservation

Allen H. Hurlbert^{*†} and Walter Jetz^{*}

^{*}National Center for Ecological Analysis and Synthesis, 735 State Street, Santa Barbara, CA 93101; and [†]Division of Biological Sciences, University of California at San Diego, La Jolla, CA 92093

Edited by Gordon H. Orians, University of Washington, Seattle, WA, and approved July 11, 2007 (received for review May 12, 2007)

Most studies examining continental-to-global patterns of species richness rely on the overlaying of extent-of-occurrence range maps. Because a species does not occur at all locations within its geographic range, range-map-derived data represent actual distributional patterns only at some relatively coarse and undefined resolution. With the increasing availability of high-resolution climate and land-cover data, broad-scale studies are increasingly likely to estimate richness at high resolutions. Because of the scale dependence of most ecological phenomena, a significant mismatch between the presumed and actual scale of ecological data may arise. This may affect conclusions regarding basic drivers of diversity and may lead to errors in the identification of diversity hotspots. Here, we examine avian range maps of 834 bird species in conjunction with geographically extensive survey data sets on two continents to determine the spatial resolutions at which range-map data actually characterize species occurrences and patterns of species richness. At resolutions less than 2° (≈200 km), range maps overestimate the area of occupancy of individual species and mischaracterize spatial patterns of species richness, resulting in up to two-thirds of biodiversity hotspots being misidentified. The scale dependence of range-map accuracy poses clear limitations on broad-scale ecological analyses and conservation assessments. We suggest that range-map data contain less information than is generally assumed and provide guidance about the appropriate scale of their use.

biodiversity | birds | geographic range | range occupancy | species richness pattern

A growing number of studies is concerned with continental-to-global scale patterns of biodiversity (1–4) or summary patterns of species' ecological traits such as body size (5) and range size (6, 7). At similarly broad scales, many conservation studies are examining the richness of rare or threatened taxa (8–11) and their distribution in relation to existing reserve networks (12–14). Over such broad geographical extents, expert-drawn range maps (extent of occurrence maps) are typically the primary source of data on species distributions, and thus taxon richness is estimated by counting the number of species ranges that overlap each cell of an underlying grid system. Of course, it has been appreciated for decades that species do not occur at all locations throughout their range (7), and recent work (15–17) has shown that discrepancies may exist between richness patterns inferred from range maps and those inferred from survey data. This mismatch has been attributed to an inherent difference in the spatial scale at which range maps and surveys capture distributional information (15). However, although the spatial scale of surveys is typically explicit in the sampling methodology (e.g., 0.1-hectare Gentry forest plots, 40-km North American Breeding Bird Survey routes, and 0.25° × 0.25° South African Bird Atlas cells), the actual scale at which range maps characterize the distribution of species is unclear (18). Despite this uncertainty, ecologists must choose a scale (or occasionally, multiple scales) at which to carry out range-map-based analyses. With the increasing availability of high-resolution climate and

land-cover data, more and more studies using range-map data are being carried out at extremely fine resolutions (Table 1).

Understanding the true ecological resolution of range-map data is critical for a number of reasons. Richness patterns are scale-dependent, with some variables being better predictors of richness at one scale and other variables better predictors at other scales (19–21). If the true resolution of range-map data differs substantially from that of the chosen grid, then attempts to explain richness using environmental data extracted at that grid resolution will suffer from a mismatch in scale. If range maps are only coarse-scale characterizations of species distribution, then their use to test hypotheses related to fine-scale mechanisms of coexistence is clearly problematic (18). In addition, a scale mismatch in spatial autocorrelation structure between predictor and response can exacerbate these effects (16). In conservation studies, analysis of range-map data at inappropriately fine resolutions may lead to the identification of erroneous “biodiversity hotspots,” overly optimistic estimates of species representation in reserves, and potentially invalid complementarity sets for identifying conservation priorities. Approaches for refining range maps to better represent actual area of occupancy exist but have only recently started to be explored (22, 23). Consequently, an understanding of the scale dependence of range-map accuracy is crucial for any analysis based on range-map data.

Previous studies (15, 24) have quantified the degree to which species are observed throughout their range by using measures of “range occupancy.” These studies found that species typically occur at 40–65% of the sites over which they are expected based on their geographic ranges, suggesting that at the resolution of these surveys, range maps are often a fairly poor characterization of distribution. Here, we perform a comprehensive analysis of the effective scale of range maps across 834 species of birds in Australia and southern Africa. We assess the congruence of range map and gridded survey (atlas) data based on species' range occupancy values and species richness patterns over six spatial resolutions ranging from 0.25° to 8° (≈25–800 km). We also examine how well range-map and atlas data agree with respect to the identification of diversity hotspots and in the perceived efficiency of the existing reserve network for protecting those hotspots.

Results and Discussion

Fine-scale atlas data illustrate the patchy and nonuniform distribution of species within their geographic range (Fig. 1A). As demonstrated by *Eremomela gregalis* in Fig. 1, at coarser spatial resolutions, range maps more accurately (but less precisely) characterize species distributions and are less prone to false absences. On average, species occurred in only 53% of the

Author contributions: A.H.H. and W.J. designed research; A.H.H. and W.J. performed research; A.H.H. and W.J. analyzed data; and A.H.H. and W.J. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[†]To whom correspondence should be addressed. E-mail: hurlbert@nceas.ucsb.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0704469104/DC1.

© 2007 by The National Academy of Sciences of the USA

Fig. 4. Boxplots reflecting the ratio between atlas- and range-map-based richness in southern Africa and Australia over six levels of spatial resolution. Asterisks denote where the distribution of atlas richness values differed significantly from the corresponding range-map richness values based on Wilcoxon signed-rank tests. **, $P < 0.0001$; *, $P < 0.001$; +, $P > 0.1$.

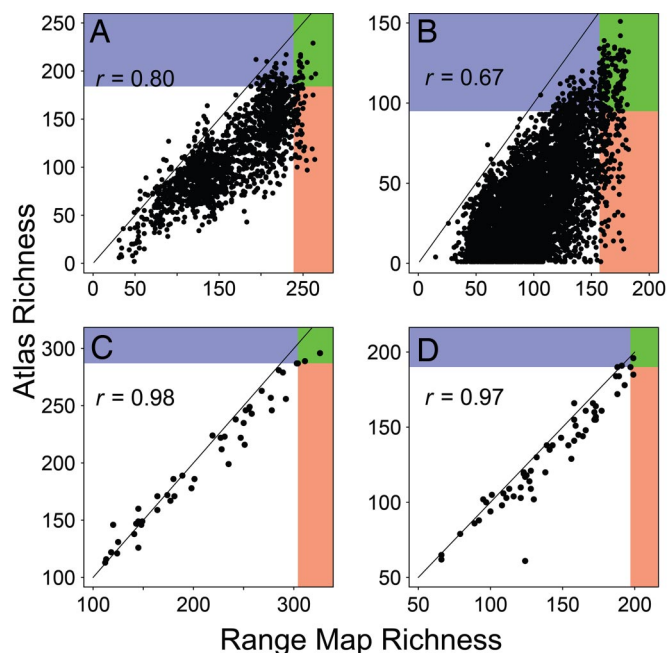


Fig. 5. The relationship between species richness based on range maps and species richness based on atlas data at 0.25° (*Upper*) and 2° (*Lower*) resolution. The solid line indicates $y = x$; the red shaded area indicates values ≥ 95 th percentile for range-map richness (range-map hotspots); blue shaded areas indicate values in the ≥ 95 th percentile for atlas richness (atlas hotspots). Green indicates where the identification of hotspots coincides. Southern Africa, $n = 1,384$ 0.25° grid cells (*A*) and $n = 45$ 2° grid cells (*C*). Australia, $n = 2,021$ 0.25° grid cells (*B*) and $n = 57$ 2° grid cells (*D*). The outlier in *D* represents a grid cell on Tasmania that also includes two pixels on the mainland.

at a fine resolution increases the sample size of the analysis without increasing the concomitant information (21). With the increasing availability of high-resolution predictor variables such as climatic and land-cover data sets, it is tempting to analyze range-map-derived ecological patterns at finer resolutions than appropriate.

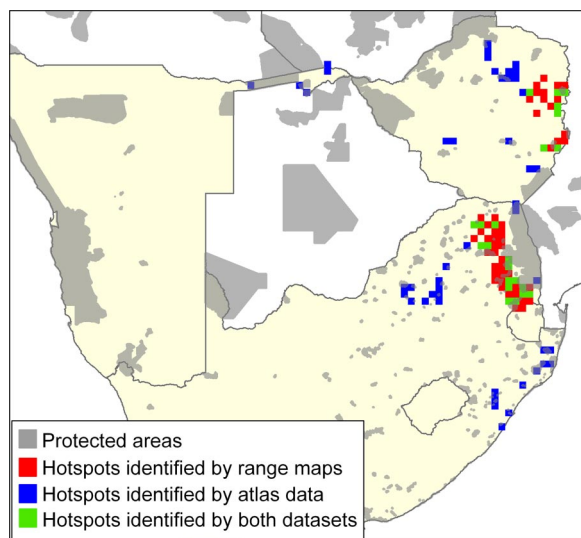


Fig. 6. Lack of congruence between atlas (blue) and range-map (red) hotspots (the 5% most species-rich grid cells) in southern Africa using 0.25° grid cells. Gray areas indicate IUCN-designated protected areas, and green grid cells represent hotspots identified by both types of data. At this resolution, only 31% of the range-map-based hotspots are also identified as hotspots by atlas data. No data were available for countries in white.

Table 2. Percent of biodiversity hotspots (the 5% richest grid cells) identified by both atlas and range-map data at four spatial resolutions for two regions

	Region	
Spatial resolution	Australia	Southern Africa
0.25°	52.2 (<i>n</i> = 249)	31.4 (<i>n</i> = 70)
0.5°	44.4 (<i>n</i> = 45)	48.4 (<i>n</i> = 31)
1°	60.0 (<i>n</i> = 15)	77.8 (<i>n</i> = 9)
2°	66.7 (<i>n</i> = 3)	100.0 (<i>n</i> = 3)

The total number of hotspots at each resolution is given in parentheses.

Our results suggest that the characterization of richness and other macroecological patterns based on range-map data at a resolution less than 2° , and certainly less than 1° , may be misleading. As such, unless refined or appropriately down-scaled to more accurately represent area of occupancy, range-map data are highly limited for addressing hypotheses that invoke local scale processes such as biotic interactions or disturbance regime. Their utility for identifying local (e.g., 100-km²) hotspots for conservation is similarly problematic. Although the results of the many recent studies conducted at 1° are likely to be qualitatively similar to the results that would be obtained at 2° , we suggest that future range-map-based studies should carry out analyses only at scales appropriate to the data. Currently, especially for less well known taxa such as amphibians or insects, this scale appears to be 2° or coarser. Our study outlines a general approach for validating range data that will aid conservation assessments as well as the pursuit of basic research in geographical ecology. It confirms the crucial need for standardized spatially extensive survey data to adequately address some of the most general and pressing questions in these fields.

Data and Methods

Range-Map Data. We extracted expert-opinion maps of bird ranges from regional sources. Only breeding ranges were included, and all species that feed predominantly in open water habitat were excluded from the analysis. Additionally, the following groups are known to have different detection probabilities in surveys and were therefore excluded: Nightjars and Allies (Caprimulgiformes), Owls (Strigiformes), birds of prey (Falconides), and shorebirds (Charadriides). Range maps for nonpasserine species in both regions were taken from the *Handbook of the Birds of the World* (38–44). Range maps for southern African passerines were taken from *The Birds of Africa* (45–47). Original digital files used in these volumes were kindly provided by the respective publishers. Maps were subsequently georegistered and converted to Geographic Information Systems format. Maps for Australian passerine species were digitized by hand from Simpson and Day (48) to a projected map. The different sources for passerine and nonpasserine birds had no noticeable effects on range occupancy (effect of passerine/nonpasserine membership on range occupancy at the fine scale; southern Africa, $F_{1,435} = 0.17$, $P > 0.9$; Australia, $F_{1,392} = 0.10$, $P > 0.9$).

Survey Data. We use two broad-scale regional bird atlases, one for the Australian continent and one for southern Africa. The advantage of survey data collected over a standardized atlas grid is that the data are easily rescaled to coarser resolutions by aggregating grid cells. Survey data for the spring and summer months (October through March) in Australia were provided by the Australian Atlas team across 25×25 km (625 km²) equal-area grid cells (49). Atlas data for the spring and summer in southern Africa were extracted from the recent bird atlas conducted across 0.25° latitude–longitude squares in Mozambique, South Africa, Swaziland, Lesotho, Namibia, and Zimbabwe (50). The area of southern African 0.25° atlas grid

cells used in the analysis varied from 636 km² for the southernmost to 742 km² for the northernmost grid cells. This degree of variation is negligible in broad-scale analyses of species richness (51). Furthermore, species with ranges restricted to the larger-grid cells in the northern half of the survey area did not have higher values of range occupancy than species with ranges restricted to the southern half of the region, as would be predicted under a grid cell area bias (mean range occupancy of northern species = 0.47; mean range occupancy of southern species = 0.57, $t = 1.55$, $df = 48.72$, $P = 0.13$). The difference in grid-cell area of up to 19% between Australia and southern Africa is trivial relative to the 4-fold variation in area across levels of scale that we examine, and thus we treat the two data sets as being of essentially equal scale and for simplicity refer to scale using the measure in degrees (0.25°, 0.5°, 1°, etc.).

We excluded a number of species from analyses ($n = 5$ in Australia, $n = 18$ in southern Africa) for which there was a major mismatch in distribution between the range maps and the atlas data. Mismatches could be due to errors in the range maps themselves, errors in the process of digitization, or inclusion of atlas occurrences outside of the breeding season. We also excluded species ($n = 12$ in Australia, $n = 11$ in southern Africa) with geographic ranges spanning <40 atlas grid cells ($\approx 25,000$ km²), because range-map uncertainty will have a greater effect on range occupancy values for narrowly ranged species. In total, we analyzed 399 species from Australia and 435 species from southern Africa.

Analysis. For analysis, range maps and atlas grid cells were geographically overlaid, resulting in a list of survey and range-map presence records for each 0.25° atlas grid cell. Range occupancy measures the extent to which species are reliably observed throughout their range (15). For any given spatial scale, range occupancy was calculated by dividing the number of atlas cell occurrences of a species by the total number of surveyed atlas cells falling within the species' geographic range. In all atlas assessments of this type, survey effort varies from region to region, which may potentially introduce bias; grid cells that are poorly surveyed are more likely to register false absences. Thus, for a particular species, all atlas cells identifying it as present were used regardless of survey effort, whereas only grid cells with at least 20 surveys were used to characterize a species' absence. This measure is more conservative with respect to false absences than one including only observed presences in well surveyed cells. Using this survey threshold, there was no relationship between the average number of surveys per grid cell across a species' geographic range and the estimate of range occupancy for that species (southern Africa, $r = 0.04$, $P = 0.48$; Australia, $r = -0.03$, $P = 0.49$). Range occupancy values based on other survey level thresholds (from 10 to 50 surveys per pixel) yielded qualitatively similar results.

Range-map and atlas data at the finest resolution (0.25° pixels)

were scaled out to coarser resolutions of 0.5, 1, 2, 4, and 8°, and a species was recorded as present in a coarse grid cell if it was present in any constituent pixel. In scaling out atlas data, a species was considered absent from a coarse grid cell if it was not observed in any surveys within the cell, and at least half of the constituent pixels had been surveyed with an average of at least 20 surveys per pixel.

For any given spatial resolution, the range-map richness of a grid cell was calculated as the total number of species to occur on at least one pixel within that cell. Calculating the atlas-based richness of coarse-resolution grid cells is complicated by the fact that grid cells vary in the total number of surveyed pixels as well as the mean number of surveys per pixel. We used the same survey constraints as for the calculation of range occupancy, including only grid cells that had at least one-half of their constituent pixels surveyed with an average of at least 20 surveys per pixel. Nevertheless, variation in the number of surveys can still affect estimates of atlas-based species richness per grid cell, and thus in addition to examining atlas richness, we also considered the residuals of atlas richness after controlling for the total number of surveys conducted in the grid cell [see [supporting information \(SI\) Table 4 and SI Appendix](#) for a more detailed description of these results].

Survey Threshold. The results presented in this study hinge on the correct identification of absences in species' distributions. As a result, the threshold number of surveys used to determine which grid cells were adequately surveyed can affect the distribution of range occupancy values as well as estimates of atlas richness, and a tradeoff exists between the survey-effort threshold and the number of grid cells that can be used in analyses. We chose a threshold that we felt represented a reasonable balance between the thoroughness of grid-cell sampling and the spatial coverage of qualifying grid cells, and our results were robust to a broad range of potential survey effort thresholds (see [SI Appendix](#)). Our results are also consistent with analyses of North American birds (15) that found values of range occupancy similar to those described here, even when an absence was characterized over a smaller area (and therefore easier to census) and over 10 years' worth of surveys. In addition, interspecific variation in range occupancy can be explained by ecological traits such as niche breadth (24), confirming a theoretical expectation for why some ranges are "holier" than others.

We thank Lauren Buckley, Jonathan Davies, Frank LaSorte, Daniel Kissling, and especially Ethan White for providing comments on an earlier draft of this manuscript. We also thank the researchers who have contributed to the collection and dissemination of the bird atlas data used here. A.H.H. was supported as a Postdoctoral Associate at the National Center for Ecological Analysis and Synthesis, a center funded by National Science Foundation Grant DEB-0072909, and the University of California, Santa Barbara. This material is partly based on work supported by National Science Foundation Grant BCS-0648733 (to W.J.).

- Buckley LB, Jetz W (2007) *Proc R Soc London Ser B* 274:1167–1173.
- Francis AP, Currie DJ (2003) *Am Nat* 161:523–536.
- Bellwood DR, Hughes TP, Connolly SR, Tanner J (2005) *Ecol Lett* 8:643–651.
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, et al. (2003) *Ecology* 84:3105–3117.
- Olalla-Tarraga MA, Rodriguez MA, Hawkins BA (2006) *Global Ecol Biogeogr* 33:781–793.
- Graves GR, Rahbek C (2005) *Proc Natl Acad Sci USA* 102:7871–7876.
- Rapoport E (1982) *Areography: Geographical Strategies of Species* (Fundación Bariloche by Pergamon Press, New York).
- Grenyer R, Orme CDL, Jackson SF, Thomas GH, Davies RG, Davies TJ, Jones KE, Olson VA, Ridgely RS, Rasmussen PC, et al. (2006) *Nature* 444:93–96.
- Ceballos G, Ehrlich PR (2006) *Proc Natl Acad Sci USA* 103:19374–19379.
- Lamoreux JF, Morrison JC, Ricketts TH, Olson DM, Dinerstein E, McKnight MW, Shugart HH (2006) *Nature* 440:212–214.
- Orme CDL, Davies RG, Burgess M, Eigenbrod F, Pickup N, Olson VA, Webster AJ, Ding TS, Rasmussen PC, Ridgely RS, et al. (2005) *Nature* 436:1016–1019.
- Ceballos G, Ehrlich PR, Soberon J, Salazar I, Fay JP (2005) *Science* 309:603–607.
- Balmford A, Moore JL, Brooks T, Burgess N, Hansen LA, Williams P, Rahbek C (2001) *Science* 291:2616–2619.
- Rodrigues ASL, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Cowling RM, Fishpool LDC, da Fonseca GAB, Gaston KJ, Hoffmann M, et al. (2004) *Nature* 428:640–643.
- Hurlbert AH, White EP (2005) *Ecol Lett* 8:319–327.
- McPherson JM, Jetz W (2007) *Glob Ecol Biogeogr*, in press.
- Graham CH, Hijmans RJ (2006) *Glob Ecol Biogeogr* 15:578–587.
- Lawes MJ, Piper SE (1998) *South Afric J Sci* 94:207–210.
- Rahbek C, Graves GR (2001) *Proc Natl Acad Sci USA* 98:4534–4539.
- Hurlbert AH, Haskell JP (2003) *Am Nat* 161:83–97.
- Rahbek C (2005) *Ecol Lett* 8:224–239.
- Ferrier S, Powell GVN, Richardson KS, Manion G, Overton JM, Allnutt TF, Cameron SE, Mantle K, Burgess ND, Faith DP, et al. (2004) *BioScience* 54:1101–1109.
- Jetz W, Wilcove DS, Dobson AP (2007) *PLoS Biol* 5:1211–1219.

24. Hurlbert AH, White EP (2007) *Glob Ecol Biogeogr*, in press.
25. McPherson JM, Jetz W, Rogers DJ (2006) *Ecol Model* 192:499–522.
26. Brooks TM, Mittermeier RA, da Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues ASL (2006) *Science* 313:58–61.
27. Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) *Nature* 403:853–858.
28. Larsen FW, Rahbek C (2003) *Biodivers Conserv* 12:599–614.
29. Shriner SA, Wilson KR, Flather CH (2006) *Ecol Appl* 16:1660–1673.
30. Chape S, Blyth S, Fish L, Fox P, Spalding M (2003) *2003 United Nations List of Protected Areas* (International Union for Conservation of Nature and Natural Resources, Gland, Switzerland, and United National Monitoring Programme World Conservation Monitoring Centre, Cambridge, UK), pp ix, 44.
31. Gaston KJ (2003) *The Structure and Dynamics of Geographic Ranges* (Oxford Univ Press, Oxford, UK).
32. Brown JH (1995) *Macroecology* (Univ of Chicago Press, Chicago).
33. Ding TS, Yuan HW, Geng S, Koh CN, Lee PF (2006) *J Biogeogr* 33:683–693.
34. Lees DC, Kremen C, Andriamampianina L (1999) *Biol J Linn Soc* 67:529–584.
35. Lyons SK, Willig MR (2002) *Ecology* 83:47–58.
36. Hawkins BA, Diniz-Filho JAF, Jaramillo CA, Soeller SA (2006) *J Biogeogr* 33:770–780.
37. Shvarts EA, Pushkaryov EV, Krever VG, Ostrovsky MA (1995) *J Biogeogr* 22:907–914.
38. del Hoyo J, Elliott A, Sargatal J (1992) *Handbook of the Birds of the World* (Lynx Edicions, Barcelona), Vol 1.
39. del Hoyo J, Elliott A, Sargatal J (1996) *Handbook of the Birds of the World* (Lynx Edicions, Barcelona), Vol 3.
40. del Hoyo J, Elliott A, Sargatal J (1997) *Handbook of the Birds of the World* (Lynx Edicions, Barcelona), Vol 4.
41. del Hoyo J, Elliott A, Sargatal J (1999) *Handbook of the Birds of the World* (Lynx Edicions, Barcelona), Vol 5.
42. del Hoyo J, Elliott A, Sargatal J (2001) *Handbook of the Birds of the World* (Lynx Edicions, Barcelona), Vol 6.
43. del Hoyo J, Elliott A, Sargatal J (2002) *Handbook of the Birds of the World* (Lynx Edicions, Barcelona), Vol 7.
44. Elliott A, Sargatal J, del Hoyo J (1994) *Handbook of the Birds of the World* (Lynx Edicions, Barcelona), Vol 2.
45. Fry CH, Keith S, Urban EK (2000) *The Birds of Africa* (Academic, London), Vol 6.
46. Keith S, Urban EK, Fry CH (1992) *The Birds of Africa* (Academic, London), Vol 4.
47. Urban EK, Fry CH, Keith S (1997) *The Birds of Africa* (Academic, London), Vol 5.
48. Simpson K, Day N (2004) *Birds of Australia* (Princeton Univ Press, Princeton, NJ).
49. Barrett G, Silcocks A, Barry S, Cunningham R, Poulter R (2003) *The New Atlas of Australian Birds* (Birds Australia, Melbourne).
50. Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown, CJ, eds (1997) *The Atlas of Southern African Birds* (Birdlife South Africa, Johannesburg).
51. Nogués-Bravo D, Araújo MB (2006) *Glob Ecol Biogeogr* 15:452–460.